

## THE PROBLEM OF HOMOPLASIES IN NEANURINAE (INSECTA: COLLEMBOLA): MICROCOMPUTER ASSISTED PHYLOGENY OF THE GENUS *DEUTONURA*

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**Summary** - Phylogenetic analysis of the genus *Deutonura* was carried out using different programs and character assumptions. Because of the high proportion of homoplastic characters, a large number of equally parsimonious trees was found in all cases. It was impossible to estimate representativeness of these tree populations. Consensus trees were poorly informative in such conditions. Numbers of available trees were too high to be properly compared. Considering however that this diversity was mainly supported by swapping between a few species and by the choice of initial assumptions, a selection of parsimonious trees was discussed. Distribution data fitted fairly well to all cladograms; Koreo-Japanese species and relictual European species were attached near the tree-root, whereas most European species formed a large monophyletic group.

I presented recently a phylogenetic tree of the palearctic genus *Deutonura* (Deharveng, 1986). This tree was built by hand using a derivate of Gisin's "Systématique Idéale" (Gisin, 1960), the only method used hitherto by collembologists for reconstructing phylogeny of species (Da Gama, 1969). Several equally parsimonious trees were obtained as a consequence of the parallel evolutions of a number of characters. Preliminary analyses carried out on other Neanurinae genera (*Endonura*, *Paleonura* and *Paranura*) showed that similar problems frequently occurred in the subfamily. As several microcomputer programs are now available for phylogenetic reconstructions, it was interesting to reconsider the question using such tools.

### MATERIAL AND METHODS

The matrix used in 1986 has been modified by the addition of several species and characters (Table 1). All known *Deutonura* are not however included because of lack of morphological data.

#### Programs

Two different programs were used :

- 1) Hennig86 v.1.5 of Farris on a very basic PCcompatible Tandy 1000 with 640 Ko memory. With such large a matrix, the options which guarantee to find the most parsimonious trees cannot be used. This limitation is documented in Hennig86 booklet. In practice, less efficient but much faster methods are usually chosen and are found to be satisfactory.
- 2) MacClade v.2.1 of Maddison and Maddison on a Macintosh SE with 1000 Ko

	*a	b	c	*d	*e	*f	g	*h	i	j	*k	*l	*m	m'	*n	o	p	*q	r	s	t	u	v	w	x	y	z	aa	ab	ac	ad	ae	af	ag	ah	ai	A	B	C	D	E	F	G	H	I	J	
abietis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	
A. alba	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0	
albella	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0
anophthalma	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	1	1	0	1	0	0	1	1	1	?	1	0	1	0	
atlantica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	1	?	1	0	1	0	1	0	
betica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	0	1	1	1	1	0	1	0	1	
binatuber	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
caerulescens	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	1
caprai	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	?	0	?	?	?	?	0	0	1	?	?	0	1	1	0	?	?	1	?	?	?
carinthiaca	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0	1	0	1	1	0	
centralis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0
coiffalti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0	1	1	0	1	0	1	0
conjuncta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	1	1	1	1	1	1
czarnohorensis	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	1	0	0	1	1	1	1	1	1	0
d.deficiens	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	0	1	0	1	1	1	0	1	0	1
d.meridionalis	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	1	1	0	1	0	1	1	1	0	1	0	
d.sylvatica	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	0	1	0	1	1	1	0	1	0	
decolorata	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	1	0	0	1	0	1	0	1	0	1	1	1	0	1	0
dextra	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0
frigida	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	
gislini	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	1	0	0	0	1	0	0	1	1	1	1	1	0	1	0	
igilica	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	?	?	0	?	?	?	?	0	0	0	?	?	0	0	1	0	?	?	?	?	?	
ilvatica	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	?	?	0	?	?	?	?	0	0	0	?	?	0	0	1	1	?	?	?	?		
*inopinata	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	1	0	0	1	0	1	0	0	1	1	1	1	0	1	0	
insularis	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0
leel	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
luberionens	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	1	1	1	?	1	0	
mirabilis	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	1	0	0	0	
*monticola	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	1	1	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
C. najtae	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0
oglasicola	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	?	?	0	?	?	?	?	0	0	0	?	?	0	0	1	0	?	?	?	?		
phlegraea	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	1	0	0	0	1	1	0	0	1	1	1	1	1	0	1	0
plena	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	
*provincialis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	
quinquesetosa	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	1	1	1	?	1	0	1	0
selgae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	1	1	1	?	1	1	1	0	
similis	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	1	1	0	1	0		
stachi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	
sylviae	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	?	?	?	?	0	0	1	?	?	?	?	1	1	?	0	1	?	?	
urbionensis	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	0	0	1	0	?	1	1	1	0	1	0	1	0
vallespirensis	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	1	1	0	1	0	

Table 1 - Complete data matrix for cladistic analysis of *Deutonura*, *Albanura* and *Catalanura*. \*, species and characters not used (cf text)

Table 2 - Remaining characters after matrix pruning, with weights and transformation polarities. S.W.: stabilized weights obtained at the 5th cycle using Successive Weighting option under Hennig86 (Table 3); R. G.: weighting by the method of Related Genera (cf text). Abbreviations: abd., abdominal tergite; Nb, number; Gr., devoid of tertiary granulation; th., thoracic tergite; tub., elementary tubercle or reticulation; X, character designation in the complete matrix; Y, character number in the pruned matrix; +, present; -, absent. Characters m' and ai to J have been added to the characters of the 1986 matrix; \*, change in polarity and coding from the 1986 matrix.

X	Y	weighting method		Transformation states (0:primitive, 1:derived)
		S.W.	R.G.	
b	1	2	1	O on head (+:0, -:1)
c	2	10	2	C on head (+:0, -:1)
g	3	0	3	DL3 on head (+:0, -:1)
i	4	0	2	Di on th.I (1seta:0, 2setae:1)
j	5	1	2	De3 on th.II (+:0, -:1)
m'	6	0	1	De3 on th.III (+:0, -:1)
o	7	0	2	De3 on abd.I-III (+:0, -:1)
p	8	0	1	Di3 on abd.V (+:0, -:1)
r	9	0	2	DF tub. on head (-:0, +:1)
s	10	0	2	BE tub. on head (-:0, +:1)
t	11	0	1	DE tub. on head (-:0, +:1)
u	12	0	1	EE tub. on head (-:0, +:1)
v	13	10	2	Gr.area between A & B on head (-:0, +:1)
w	14	2	2	Gr.area between C & F on head (+:0, -:1)
x	15	0	2	Af and Oc on head (separate:0, fused:1)
y	16	10	3	Antero-internal tub. of DL on head (-:0, +:1)
z	17	10	3	Di tub. on th.I (-:0, +:1)
aa	18	10	3	Di and De tub. on th.I (separate:0, fused:1)
ab	19	2	3	*S-De2 tub. on th.II-III (-:0, +:1)
ac	20	4	2	De2-De3 tub. on th.II-III (-:0, +:1)
ad	21	4	2	De2-De3 tub. on abd.I-III (-:0, +:1)
ae	22	0	1	Di tub. on abd.IV (separate:0, fused:1)
af	23	0	1	Eyes (+:0, -:1)
ah	24	2	2	Labrum (not pointed:0, pointed:1)
ai	25	3	2	Di3 on th.II-III (free:0, not free:1)
A	26	10	3	Fictive character marking genetic compatibility between <i>deficiens</i> , <i>meridionalis</i> and <i>sylvatica</i> , coded 0 for these species and 1 for the others.
B	27	2	3	AA tub. on head (-:0, +:1)
C	28	3	2	Ae tub. on head (-:0, +:1)
D	29	1	2	Nb of tub. between A setae on head (0-1:0, 2:1)
E	30	4	2	Di2 on abd.IV (on the edge of tub.:0, within tub.:1)
F	31	1	1	Nb of tub. between Di2 setae on abd.V (1-2:0,3-4:1)
G	32	0	3	DL1 on head (on the edge of tub.:0, within tub.:1)
H	33	0	1	Nb of antero-internal tub. of DL on head (1:0, >1:1)
I	34	10	2	Tub. anterior to De2 setae on abd.IV (-:0, +:1)
J	35	10	2	Nb of tub. anterior to De2 setae on abd.IV (<4:0, >4:1)

memory. This program has not the capabilities of Hennig86 to produce parsimonious trees, but it allows easy interactive branch-rearrangements in a given tree and quick changes in character assumptions.

#### Outgroup

The hypothetical ancestor, in which all character states were considered as primitive and coded 0, was selected as outgroup in all analyses.

#### Characters

Characters and their states are detailed in Deharveng, 1986, and on table 2 for the 11 new characters introduced in the present analyses.

#### Coding the characters

Every character was coded 0 or 1; transformation series of characters were dissociated into different characters coded 0 or 1 before integrating in the matrix. The polarity of character states is exposed in Deharveng(1983, 1986) and in table 2.

Polymorphic characters, which can exist in states 0 and 1 in the same species, can be coded as such only with MacClade. To preserve the homogeneity of the matrix used for analyses in both programs, there were two solutions:

- 1) omitting the character, which would result in a loss of information;
- 2) coding the character as 0. The 2 morphotypes which represent the polymorphic species are phylogenetically undissociated; so, it is possible to retain only the more primitive one in which the character is at state 0. However, the removal of the derived morphotypes results in decrease in the real number of homoplasies. A bias is thus introduced in a subsequent weighting of characters using methods such as Successive Weighting of Farris, which depend on the importance of homoplasies in the trees (cf below).

#### Weighting the characters

Various methods have been proposed for character weighting (Sharkey, 1989); I used the option Successive Weighting of Hennig86 (S.W.). This method weights the characters "according to their fit to the trees in the input tree file" (Farris, 1988); then, the next run is made with the weighted characters and gives a new population of parsimonious trees; from this second tree population, a new set of weights is obtained and again a new run is achieved. The operation is repeated until the weights are stabilized in successive cycles.

Character weights obtained at the close of a run using Successive Weighting option would best be compared with weights derived from an other weighting method. A weighting indexed on the frequency of homoplasies of the character in related genera (R.G. method) was considered to be convenient here. However, as information is limited for the genera near *Deutonura* (*Endonura*, *Neanura*, *Protonura*), only a rough estimate of the character weights on a scale 1 to 3 is proposed (Table 2).

#### Reversibility of character transformations

Characters evolution is considered to be reversible (transformations from state 0 to state 1 and from state 1 to state 0 are both possible) in Hennig86, but MacClade accepts also irreversibility. It is intuitively clear for taxonomists

that some characters are likely to be irreversible during evolution such as eye reduction; it is thus necessary to check carefully the distribution of such characters in the final trees obtained with Hennig86 in order to detect questionable reverse transformations.

### Species

Forty-one species have been analysed; the following were added to those of the 1986 matrix:

- five species described from Sardinia by Dallai (1983): *Deutonura caprai*, *igilica*, *ilvatica*, *oglasticola* and *sylviae*;
- two species isolated in the genus (*D. centralis* Gama, 1964 from Portugal and Spain and *D. mirabilis* Deharveng, 1987 from an Austrian cave);
- two species which belong to small genera rather closely related to *Deutonura*: *Albanura alba* Deharveng, 1982 from Albania and *Catalanura najtae* Deharveng, 1979 from Catalonia.

### Simplifying the matrix

The complete matrix (41 species x 47 characters, table 1) contains a number of characters and species which do not contribute to the resolution of the tree, but make the run longer and the log files of results larger. These elements can be removed for the analysis, and easily replaced in the final tree. They are:

- 1) autapomorphic characters which exist in the primitive state in all but one species (characters a, d, e, f, h, k, l, m, n, q); they do not contribute to the dichotomic resolution of the trees, which is only determined by synapomorphies;
- 2) duplicate characters which exhibit the same state distribution in the set of taxa;
- 3) duplicate species which have the same character states distribution as other species (*D. conjuncta/provincialis/monticola*; *D. gisini/inopinata*).

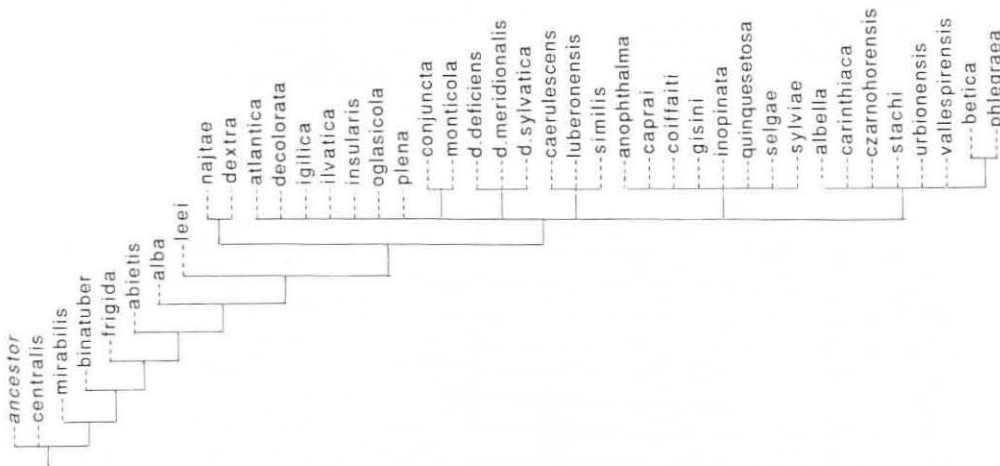


Figure 1 - Terminal consensus tree of the genus *Deutonura* analysed by Hennig86 (nelsen command, table 3).

Table 3 - Details of a run using Successive Weighting option under Hennig86. CI: consistency index = sum of the number of possible transformations for each character/length of the tree; >, means overflow. Commands (after Farris, 1988):

m, "constructs several trees, each by a single pass" through the data, "adding the terminals in several different sequences; the shortest trees found are retained";

m\*, "applies branch-swapping to each of the initial trees, retaining no more than 1 tree for each initial one";

bb\*, "applies extended branch-swapping to the trees in the current tree file, producing a new tree file; the shortest trees found are retained"; bb\*, "will use all available tree space, if necessary, to store its results";

xs w "sets the characters' weight according to their fit to the trees in the input tree file";

cc, lists "the calculated weights";

nelsen, "calculates the Nelson consensus tree of the trees in the current tree file".

Cycle	Command	Execution time in sec	Tree length	Consistency index	Tree number
1	m bb* xs w cc	1235.9 97.7 1.3	99 99	35 35	3 >100
2	m* bb* xs w cc	671.5 39914.6 2262.3 1.4	206 206	50 50	>5 >2278
3	m* bb* xs w cc	472.9 32905.8 2218.9 1.3	169 169	57 57	>5 >2278
4	m* bb* xs w cc	490.2 54166.0 2187.7 4.6	181 181	62 62	>5 >2278
5	m* bb* xs w cc	305.6 23537.8 1969.0 4.6	161 161	68 68	>5 >2278
6	m*	298.3	161	68	>5
	nelsen	110.8			
Total		162559.9	i.e. 45 hr, 9mn, 19.9s		

Table 4 - Runs performed under MacClade. Character assumptions: r, reversible; i, irreversible; 1, equal weighting; p, weighting according to Related Genera method.

Tree	Length	C.I.	Assumptions	Topology and tree processing
1R	106	0.33	r,1	from analysis1 (Hennig86), cycle 5
2R (Fig.2)	99	0.35	r,1	Branch-swapping on tree 1R
2I	150	0.23	i,1	= tree 2R
3I (Fig.5)	120	0.29	i,1	Branch-swapping on tree 2I
R3	181	0.38	r,p	= tree 2R
R4 (Fig.3)	180	0.38	r,p	Branch-swapping on tree 2R
4I	282	0.24	i,p	= tree R4
5I (Fig.4)	216	0.32	i,p	Branch-swapping on tree R4

At last, the character ag (pigment loss) occurs in so many different lines of Neanurinae that it was removed from the matrix.

The pruned matrix had 38 species for 35 characters (Table 1).

## RESULTS

### Analysis 1 with Hennig86 using Successive Weighting option

All characters are equally weighted at the opening of the run. The results are summarized on table 3, and the last consensus tree obtained by the nelsen command is represented on figure 1.

### Analysis 2 with Mac Clade

One of the most parsimonious trees obtained under Hennig86 is transferred to Mac Clade and processed according to different combinations of the character assumptions (table 4): reversible/irreversible and equal weight/weight after R.G. method. Branch-swapping is applied in each case to improve the tree. Examples of the shortest trees, among a number of equally parsimonious ones, are given on figures 2 to 5. The tree of figure 5 (under assumptions of irreversible transformations and equal weighting) has been completed with the species and the characters previously pruned out of the original matrix.

## DISCUSSION

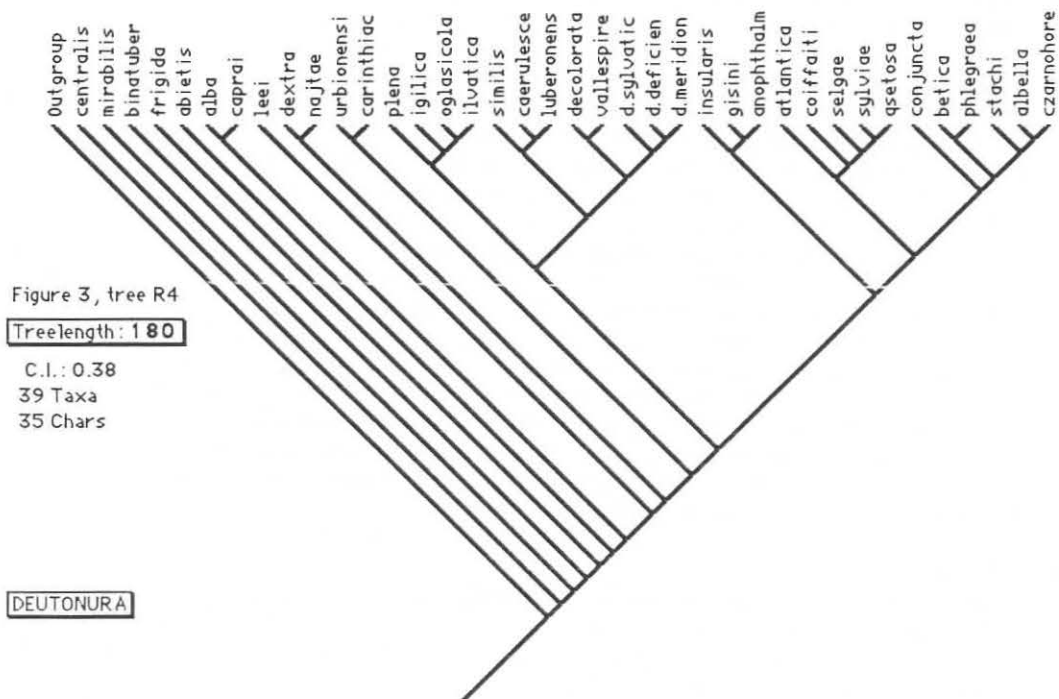
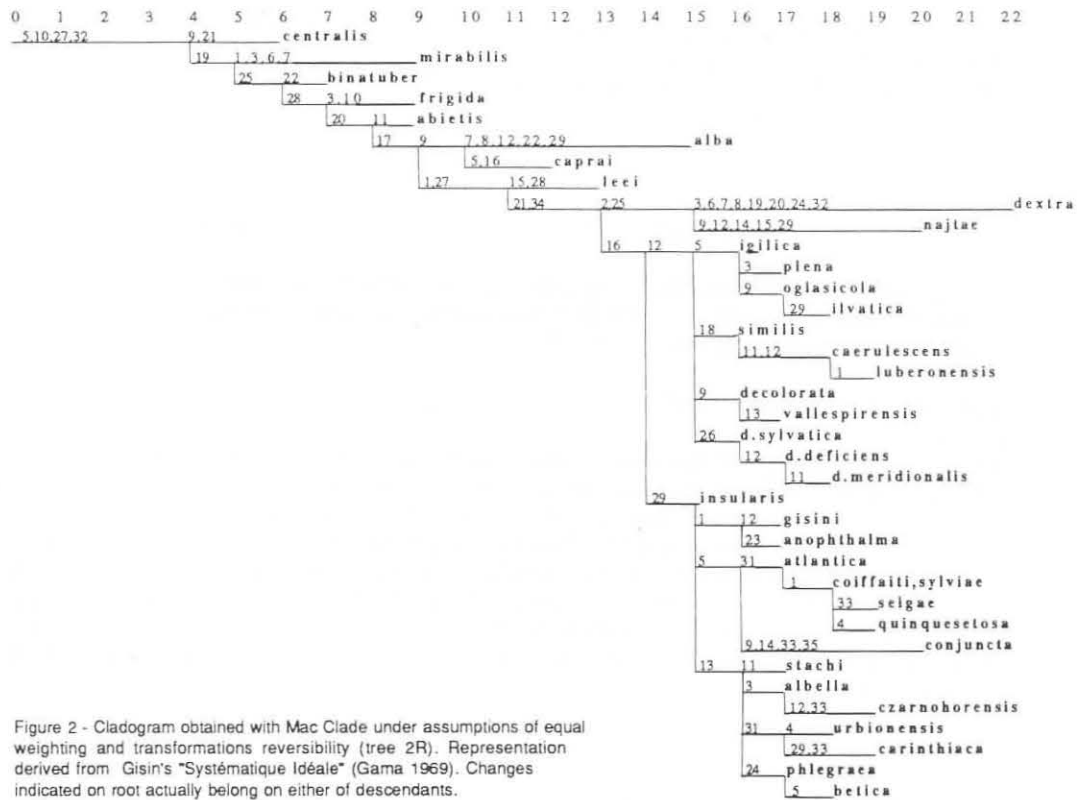
### Representativity of the trees

It is clear that the best trees are strongly dependent on the initial character assumptions. A tree topology, parsimonious under given character assumptions, can be far from parsimonious when transferred under other character assumptions (Table 4). As objective comparison criterions are not available (in particular, tree length is dependent on weighting), the final choice between these different trees amounts finally to a choice between different assumptions, as far as we are certain of the parsimony of the trees.

An other problem arises here. The mathematical processing of a large and complex data set like the present one can only be done by programs or options which do not guarantee to find the best trees, although they are likely to do so (Platnick, 1988). Their efficiency decreases also with the complexity of the data, whereas execution time increases. Hennig86, which is considered to be a fast program (Platnick, 1988), ran more than 45 hours to process the *Deutonura* matrix (Table 3).

On the other hand, the most parsimonious trees are legion; nevertheless, it was impossible to obtain either all the equally parsimonious trees of a cycle or even their total number, due to hardware limitations. Had all the most parsimonious trees been considered in the analysis with Hennig86, character weighting could have been different and also the final best trees. So, we have no idea at what extent the available trees are representative of the complete population of most parsimonious trees.

Given these limitations, it is advisable to be cautious before taking any taxonomic decision based on the results of a phyletic analysis in a genus affected by frequent homoplasies during evolution like *Deutonura*. The different parsimonious trees of figures 1 to 5 which are analysed below can only be considered as phyletic hypotheses among others.



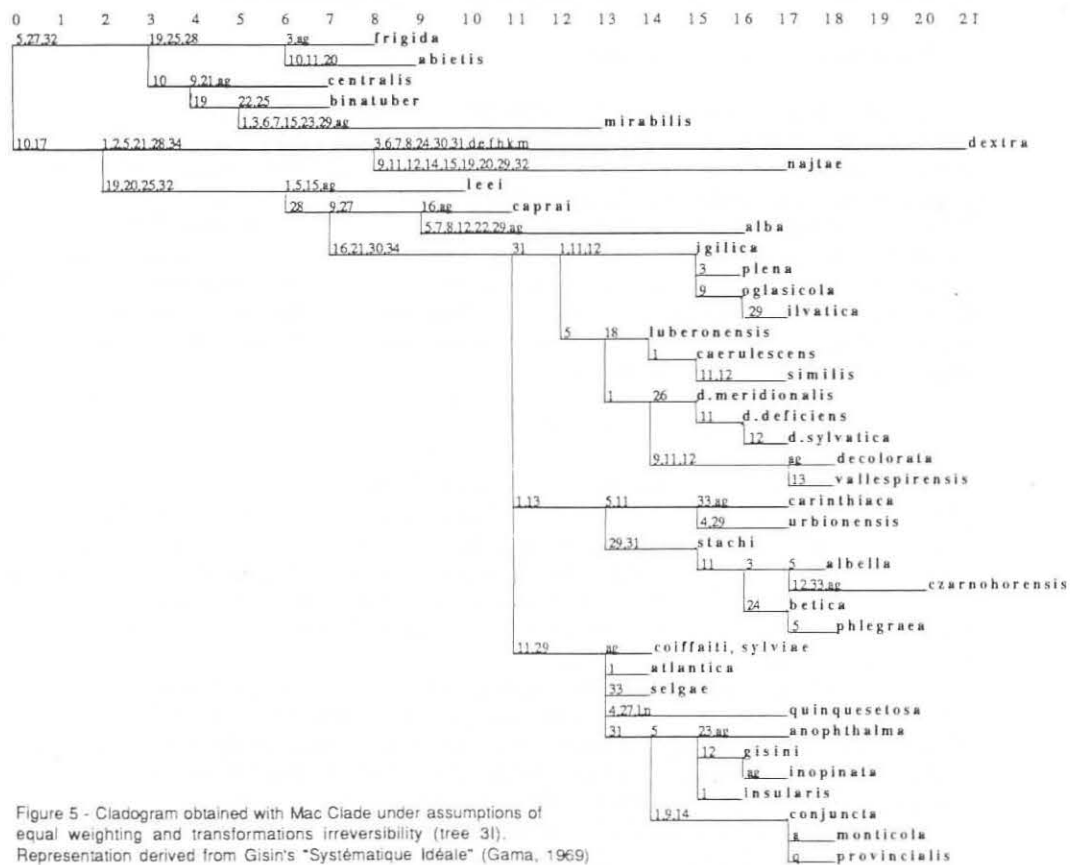
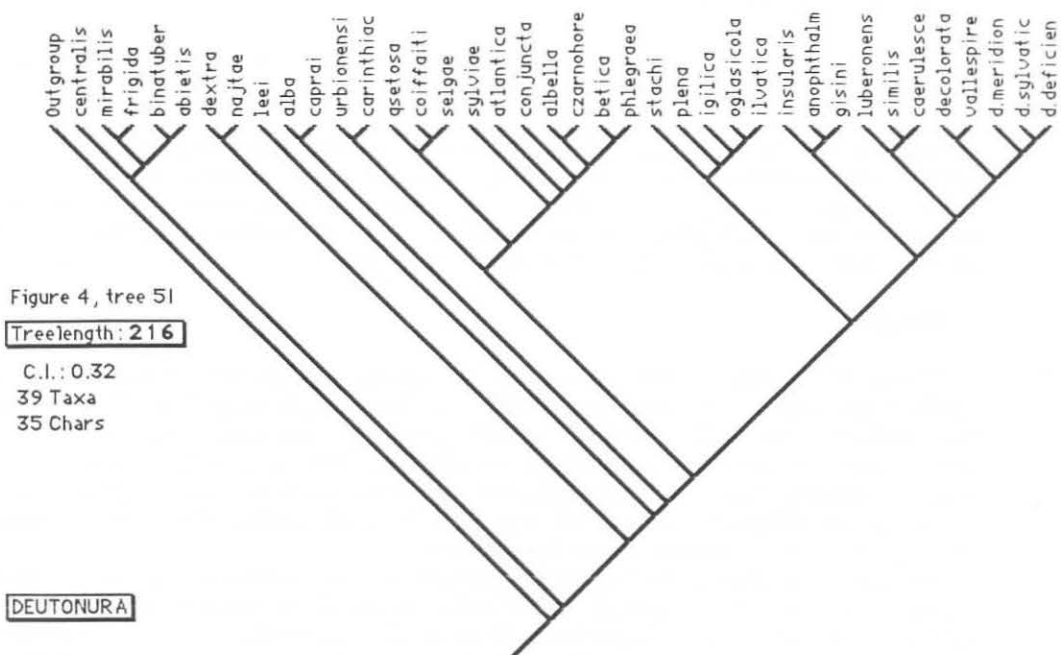


Figure 5 - Cladogram obtained with Mac Clade under assumptions of equal weighting and transformations irreversibility (tree 31). Representation derived from Gisin's "Système Idéale" (Gama, 1969)

## Structure of the trees

Most differences in tree topology rest on limited terminal branch-swapping; the branching near the root of the trees varies also according to the initial character assumptions. The consensus tree (fig.1) is loosely structured (independent branching of some species near the root and a few distal polychotomies with remaining species) and poorly informative. But some features emerge constantly from the different runs: several species groups in the cladogram canopy, and a large monophyletic group branching above either *A.alba*-*D.caprai* or *C.najtae*-*D.dextra*.

## Weights

Character weights from Successive Weighting option of Hennig86 and R.G. method are often very different (Table 2). The rough way I used to determine the weights in R.G. method could possibly account in part for these differences. A second explanation would be that a given character exhibit quite different rates of homoplasies in *Deutonura* and in other genera, resulting in different weighting under S.W. and under R.G.. Hard data are lacking to test seriously these hypothesis.

At least, a major discrepancy concerning the character g could provide support for the R.G. method. DL3 seta on head is present in all Neaurini species, except three Carpathian *Deutonura* (*albella*, *czarnohorensis* and *plena*); thus, it was given the maximum weight under R.G; in contrast, its weight under S.W. was 0, in discordance with distribution data.

## Transformations reversibility

In the parsimonious tree 2R selected as example (Fig.2), 13 characters were affected by reversions. Among these, only the characters 1 and 5, which show frequent fluctuations in many genera of Neaurinae, can be easily accepted as reversible during evolution. Status of characters 29 and 31 is less clear. All other characters (10, 11, 12, 19, 20, 25, 27, 28, and 32) are related to tubercle differentiation, the evolution of which was considered to be irreversible on the ground of clear clinal variations (Deharveng, 1984). More detailed investigations are consequently needed about tubercle differentiation reversibility (and more generally characters reversibility) during evolution of *Deutonura*.

## Fitting to biogeographical data

On the whole, geographic distributions are consistent with species grouping. All Koreo-Japanese species (*D.abietis*, *D.binatuber*, *D.frigida* and *D.leei*) branch near the basis of the trees, with *D.leei* a little apart. They are more or less mixed with the morphologically atypical European species (*A.alba*, *C.najtae*, *D.caprai*, *D.centralis*, *D.dextra* and *D.mirabilis*), the relictual status of which is corroborated by distribution data (endemic species restricted to small isolated areas).

The other European species, rather similar in morphology, form the large monophyletic branch mentioned above. It contains several small species groups in the canopy which are usually biogeographically homogenous: *quinquesetosa*-*coiffaiti*-*selgae* from the Iberian peninsula; *insularis*-*gisini-anophthalma* from Southern France and Corsica; *albella*-*czarnohorensis* from Carpathian mountains; *betica*-*phlegraea* from West Mediterranean region; *igilica*-*ilvatica*-*oglasicola* from Sardinia; *d.meridionalis*-*d.deficiens*.

*d.sylvatica* from Southwestern France and adjacent area of Spain.

Some phyletic problems remains to be resolved. First, branching near the tree roots is not stabilized. The five species *D.abietis*, *D.binatuber*, *D.frigida*, *D.centralis* and *D.mirabilis* constitute a paraphyletic group if characters are considered to be reversible (Fig. 1, 2 & 3), but they are monophyletic if characters are considered to be irreversible (Fig. 4 & 5). A re-examination of the affinities between Koreo-Japanese and relictual European species would be useful and possible as several species not included in my analysis like *D.granatuberis* or *D.yoshii* are available.

Second, conflicts between phylogeny and biogeography are obvious in several terminal branches which join species such as *carinthiaca* (Austria) and *urbionensis* (Spain), or *decolorata* (Northern Alps) and *vallespirensis* (Catalonia). These distributions of supposed related taxa present such unusual patterns that the reality of the taxa affinity itself should be first questioned.

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